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A new species of *Boulenophrys* (Anura, Megophryidae) from northern Jiangxi, China

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Abstract

A new species of the genus *Boulenophrys* (Anura, Megophryidae), *Boulenophrys nebulosa* **sp. nov.**, is described from Mt. Lushan, Jiangxi Province, China. Phylogenetic analyses based on mitochondrial *COI* and *16S rRNA* genes show that the new species forms a sister lineage to *B. mufumontana*. Morphologically, *B. nebulosa* **sp. nov.** differs from all known congeners by a unique combination of characters and from its closest relative, *B. mufumontana*, by the following combination of characters: (1) relative finger lengths I < II < IV < III; (2) indistinct subarticular tubercle at the base of each finger; (3) larger male body size (SVL 31.8–32.3 mm); (4) heels just meeting when hindlimbs are folded; (5) tibiotarsal articulation reaching the center of the eye when the leg is stretched forward; and (6) vomerine teeth present. This study expands the known distribution of *Boulenophrys* in Jiangxi and provides baseline data for biodiversity conservation efforts in Mt. Lushan.

Key Words

Asian horned toads, biodiversity, *Boulenophrys nebulosa* sp. nov., taxonomy

Introduction

The genus *Boulenophrys* Fei, Ye & Jiang, 2016 (Megophryinae) currently comprises 78 recognized species (Table 1). Its members are distributed across the Himalayas, northeastern India, southern China, and Southeast Asia (Lyu et al. 2023; AmphibiaWeb 2025; Frost 2025). Despite its broad range, recent integrative studies have revealed extensive cryptic diversity within *Boulenophrys*, much of which is not discernible by morphology alone (Liu et al. 2018). These findings have spurred taxonomic revisions within the subfamily Megophryinae, with Lyu et al. (2023) proposing a ten-genus system that affirms *Boulenophrys* as the most species-rich lineage. In Jiangxi, known *Boulenophrys* species are primarily described from the Luoxiao Mountains along the Hunan border and the Wuyi Mountains along the Fujian border. However, the northern part of Jiangxi, including the topographically isolated granitic massif of Mt. Lushan in the Yangtze River Basin, has received limited herpetological attention. This suggests that the species diversity of *Boulenophrys* in this region may still be underestimated.

Historically, two *Boulenophrys* populations have been recorded in Mt. Lushan: *B. lushanensis* Shen, Zhou & Li (Shen et al. 2025), and another first reported by Yang et al. (2007), initially identified as *Megophrys minor brachykolos* (Inger & Romer, 1961) (currently *B. brachykolos*). However, once thought to be widely distributed in southern China and northern Vietnam (Fei et al. 2009), *B. brachykolos* has been restricted to Hong Kong and Shenzhen based on voucher specimens and molecular data (Lyu et al. 2023). For instance, the re-

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Table 1. References for morphological characters of 78 recognized species of *Boulenophrys*.

ID	*Boulenophrys* Species	References
1	*B. acuta* Wang, Li & Jin, 2014	Li et al. 2014
2	*B. angka* Wu, Suwannapoom, Poyarkov, Pawangkhanant, Xu, Jin, Murphy & Che, 2019	Wu et al. 2019
3	*B. anlongensis* Li, Lu, Liu & Wang, 2020	Li et al. 2020
4	*B. baishanzuensis* Wu, Li, Liu, Wang & Wu, 2020	Wu et al. 2020
5	*B. baolongensis* Ye, Fei & Xie, 2007	Ye et al. 2007
6	*B. binchuanensis* Ye & Fei, 1995	Ye and Fei 1995; Lyu et al. 2023
7	*B. binlingensis* Jiang, Fei & Ye, 2009	Fei et al. 2009; Lyu et al. 2023
8	*B. boettgeri* Boulenger, 1899	Boulenger 1899; Lyu et al. 2023
9	*B. brachykolos* Inger & Romer, 1961	Inger and Romer 1961; Lyu et al. 2023
10	*B. caobangensis* Nguyen, Pham, Nguyen, Luong & Ziegler, 2020	Nguyen et al. 2020
11	*B. caudoprocta* Shen, 1994	Shen. 1994
12	*B. cheni* Wang & Liu, 2014	Wang et al. 2014
13	*B. chishuiensis* Xu, Li, Liu, Wei & Wang, 2020	Xu et al. 2020
14	*B. congjiangensis* Luo, Wang, Wang, Lu, Wang, Deng & Zhou, 2021	Luo et al. 2021
15	*B. changyangensis* Li, Shi, Liu, Zhao, Gao, & Wang, 2025	Li et al. 2025
16	*B. daiyunensis* Lyu, Wang & Wang, 2021	Lyu et al. 2021
17	*B. dalaolingensis* Wang, Chen & Liu, 2025	Wang et al. 2025a
18	*B. daoji* Lyu, Zeng, Wang & Wang, 2021	Lyu et al. 2021
19	*B. daweimontis* Rao & Yang, 1997	Rao and Yang 1997
20	*B. daxuemontis* Liu, Li, Cheng, Wei, Wang & Cheng, 2025	Liu et al. 2025b
21	*B. dongguanensis* Wang & Wang, 2019	Wang et al. 2019a
22	*B. dupanglingensis* Xiao & Mo, 2025	Xiao et al. 2025
23	*B. elongata* Zeng, Wang, Chen, Xiao, Zhan, Li & Lin, 2024	Zeng et al. 2024
24	*B. fanjingmontis* Zhang, Liang, Ran & Shen, 2012	Zhang et al. 2012
25	*B. fansipanensis* Tapley, Cutajar, Mahony, Nguyen, Dau, Luong, Le, Nguyen,Nguyen, Portway, Luong & Rowley, 2018	Tapley et al. 2018
26	*B. fengshunensis* Wang, Zeng, Lyu & Wang, 2022	Wang et al. 2022
27	*B. frigida* Tapley, Cutaja, Nguyen, Portway, Mahony, Nguyen, Harding, Luong& Rowley, 2021	Tapley et al. 2021
28	*B. gaolanensis* Song, Wang,Qi, Wang, Wang,2024	Song et al.2024
29	*B. gutu* Kang, Wei & Shi, 2025"	Kang et al. 2025
30	*B. hengshanensis* Qian, Hu, Mo, Gao, Zhang & Yang, 2023	Qian et al. 2023
31	*B. hoanglienensis* Tapley, Cutajar, Mahony, Nguyen, Dau, Luong, Le, Nguyen,Nguyen, Portway, Luong & Rowley, 2018	Tapley et al. 2018
32	*B. huangniushiensis* Wang, Wu, Song, Huang, Zhuo, & Wang, 2025	Wang et al. 2025b
33	*B. hungtai* Wang, Zeng, Lyu, Xiao & Wang, 2022	Wang et al. 2022
34	*B. insularis* Wang, Liu, Lyu, Zeng & Wang, 2017	Wang et al. 2017a
35	*B. jiangi* Liu, Li, Wei, Xu, Cheng, Wang & Wu, 2020	Liu et al. 2020
36	*B. jingdongensis* Fei & Ye, 1983	Fei et al. 1983; Lyu et al. 2023
37	*B. jinggangensis* Wang, 2012	Wang et al. 2012
38	*B. jiulianensis* Wang, Zeng, Lyu & Wang, 2019	Wang et al. 2019a
39	*B. kuatunensis* Pope, 1929	Pope 1929; Lyu et al. 2023
40	*B. leishanensis* Li, Xu, Liu, Jiang, Wei & Wang, 2018	Li et al. 2018
41	*B. liboensis* Zhang, Li, Xiao, Li, Pan, Wang, Zhang & Zhou, 2017	Zhang et al. 2017
42	*B. lichun* Lin, Chen, Li, Peng, Zeng, Wang, 2024	Lin et al.2024
43	*B. lini* Wang & Yang, 2014	Wang et al. 2014
44	*B. lushanensis* Shen, Zhou & Li, 2025	Shen et al. 2025
45	*B. lishuiensis* Wang, Liu & Jiang, 2017	Wang et al. 2017b
46	*B. lushuiensis* Shi, Li, Zhu, Jiang, Jiang & Wang, 2021	Shi et al. 2021
47	*B. minor* Stejneger, 1926	Stejneger 1926; Lyu et al. 2023
48	*B. mirabilis* Lyu, Wang & Zhao, 2020	Lyu et al. 2020
49	*B. mufumontana* Wang, Lyu & Wang, 2019	Wang et al. 2019a
50	*B. nankunensis* Wang, Zeng & Wang, 2019	Wang et al. 2019a
51	*B. nanlingensis* Lyu, Wang, Liu & Wang, 2019	Wang et al. 2019a
52	*B. obesa* Wang, Li & Zhao, 2014	Li et al. 2014
53	*B. ombrophila* Messenger & Dahn, 2019	Messenger et al. 2019
54	*B. omeimontis* Liu, 1950	Liu 1950; Lyu et al. 2023
55	*B. palpebralespinosa* Bourret, 1937	Bourret 1937; Lyu et al. 2023
56	*B. pepe* Wang & Zeng, 2024	Wang et al. 2024
57	*B. puningensis* Wang, Zeng, Lyu, Xiao & Wang, 2022	Wang et al. 2022
58	*B. qianbeiensis* Su, Shi, Wu, Li, Yao, Wang & Li, 2020	Su et al. 2020
59	*B. rubrimera* Tapley, Cutajar, Mahony, Chung, Dau, Nguyen, Luong & Rowley,2017	Tapley et al. 2017
60	*B. sangzhiensis* Jiang, Ye & Fei, 2008	Jiang et al. 2008
61	*B. sanmingensis* Lyu & Wang, 2021	Lyu et al. 2021
62	*B. shimentaina* Lyu, Liu & Wang, 2020	Lyu et al. 2020
63	*B. shuichengensis* Tian & Sun, 1995	Tian and Sun 1995
64	*B. shunhuangensis* Wang, Deng, Liu, Wu & Liu, 2019	Wang et al. 2019b
65	*B. spinata* Liu & Hu, 1973	Hu et al. 1973; Lyu et al. 2023
66	*B. tongboensis* Wang & Lyu, 2021	Lyu et al. 2021

ID	*Boulenophrys* Species	References
67	*B. tuberogranulatus* Shen, Mo & Li, 2010	Mo et al. 2010
68	*B. wugongensis* Wang, Lyu & Wang, 2019	Wang et al. 2019a
69	*B. wuliangshanensis* Ye & Fei, 1995	Ye and Fei 1995
70	*B. wushanensis* Ye & Fei, 1995	Ye and Fei 1995
71	*B. xiangnanensis* Lyu, Zeng & Wang, 2020	Lyu et al. 2020
72	*B. xianjuensis* Wang, Wu, Peng, Shi, Lu & Wu, 2020	Wang et al. 2020
73	*B. xuefengmontis* Lyu & Wang, 2023	Lyu et al. 2023
74	*B. yangmingensis* Lyu, Zeng & Wang, 2020	Lyu et al. 2020
75	*B. yaoshanensis* Qi, Mo, Lyu, Wang & Wang, 2021	Qi et al. 2021
76	*B. yezhongensis* Liu, Feng, Shen, Li, Cheng, Wei, Wang & Su, 2025	Liu et al. 2025a
77	*B. yingdeensis* Qi, Lyu, Wang & Wang, 2021	Qi et al. 2021
78	*B. yunkaiensis* Qi, Wang, Lyu & Wang, 2021	Qi et al. 2021

cord from Mt. Dayaoshan, Guangxi, was revised and described as the new species *B. yaoshanensis* Qi, Mo, Lyu, Wang & Wang, 2021, and the record from Mt. Hengshan, Hunan, was revised as the new species *B. hengshanensis* Qian, Hu, Mo, Gao, Zhang & Yang, 2023. Consequently, all previous records of *B. brachykolos* from other regions are now considered questionable and need to be carefully re-examined. Notably, the population of *B. brachykolos* from Mt. Lushan has not yet been evaluated using genetic or detailed morphological analyses, leaving its taxonomic identity unresolved.

Herpetological surveys on Mt. Lushan since 2021 have led to the collection of several horned toad specimens. Morphological examinations revealed that these individuals could not be classified as any known species of the genus. While they share a superficial resemblance to *B. mufumontana*, they exhibit distinct differences in a combination of morphological characters, most notably in the relative length of their fingers. To further elucidate their taxonomic status, we sequenced *16S* and *COI* mitochondrial gene fragments and performed phylogenetic analyses. Integrative evidence from phylogeny and morphology supports the recognition of the Mt. Lushan population as a distinct evolutionary lineage. Based on this evidence, we formally describe it as a new species herein.

Materials and methods

Sampling

Fieldwork was conducted at Mt. Lushan, China. Seven adult specimens and one tadpole specimen were collected in April, June, and November 2021. After capture, the specimens were euthanized with tricaine methanesulfonate (MS-222). Liver or thigh muscle tissues were taken for molecular experiments, preserved in 95% ethanol, and stored at –70 °C. Whole specimens were fixed in 75% ethanol. All specimens and tissue samples were deposited in the Animal Museum of the Life Sciences College, Jiangxi Normal University (JXNU), Nanchang, Jiangxi Province, China. All animal protocols were reviewed and approved by the Animal Ethical and Welfare Committee of Jiangxi Normal University.

Morphological analyses

Morphological terminology and character definitions followed Lyu et al. (2023) and subsequent taxonomic revisions of *Boulenophrys*. External measurements were taken using a digital caliper (Neiko 01407A, stainless steel, 6-inch) to the nearest 0.1 mm. The following measurements were recorded: snout–vent length (SVL), head length (HDL), head width (HDW), snout length (SNT), internasal distance (IND), interorbital distance (IOD), eye diameter (ED), tympanum diameter (TD), tympanum–eye distance (TED), hand length (HND), forearm length (RAD), tibial length (TIB), and foot length (FTL). Sex was determined by the presence of secondary sexual characteristics, including internal vocal sac openings or nuptial pads in males, and by direct observation of courtship calling when possible (Fei et al. 2009). The presence or absence of nuptial pads was verified under a dissecting microscope. Comparative morphological data for congeners were compiled from original species descriptions and taxonomic revisions (Table 1), ensuring consistency in character definitions and measurement standards.

For the single tadpole of the undescribed species, the following morphometric characters were measured: maximum body height (BH), maximum body width (BW), interocular distance (IOS), mouth width (MW), snout length (SL), snout-to-spiraculum distance (SS), snout–vent length (SVL), tail height (TAH), tail length (TAL), maximum width of the tail base (TBW), and total length (TOL).

The morphometric measurements were statistically analyzed using Python 3.11 with the pandas, numpy, scikit-learn, and matplotlib packages. For analyses, all measurements were ln-transformed to normalize and reduce variance, and then scaled to remove allometric effects of body size using the following equation: $Xa = Xln - \beta \times (SVLln - SVLm)$, where Xa = adjusted value, Xln = ln-transformed measurement, β = unstandardized regression coefficient for each species, SVLln = ln-transformed SVL, and SVLm = overall average SVLln of all samples. The size-adjusted measurements were then standardized using z-score normalization to ensure comparability across variables. Principal component analysis (PCA) was performed to examine morphological variation among species using the PCA function from scikit-learn. Since sexual dimorphism is

common in frogs, we compiled a dataset using male specimens from the type series of *B. mufumontana* (Wang et al. 2019a) and the undescribed species for PCA.

DNA sequencing and molecular analyses

Genomic DNA was extracted from tissue samples using the Universal Genomic DNA Kit (CWBIO, Beijing, China) following the manufacturer's protocol for animal tissue. Two mitochondrial gene fragments, the partial 16S ribosomal RNA coding sequence (16S rRNA) and the partial cytochrome c oxidase subunit I gene (COI), were amplified in 50 μL reactions. Primer pairs and PCR protocols followed Liu et al. (2018).

For the phylogenetic analyses, sequences of 78 *Boulenophrys* species were obtained from GenBank, except for *B. changyangensis*, *B. dalaolingensis,* and *B. gutu* due to unavailable data. Two outgroup species, *Xenophrys glandulosa* and *X. mangshanensis*, were also included (Suppl. material 1: table S1). All sequences were aligned using the MUSCLE algorithm with default parameters. Phylogenetic analyses were conducted based on a concatenated mitochondrial dataset comprising COI and 16S rRNA genes (total length: 1,236 bp).

Both Maximum likelihood (ML) and Bayesian inference (BI) methods were employed to construct phylogenetic trees. The ML analysis was performed in IQ-TREE v3.0.1, with the best-fit substitution model (TVM+F+R5) selected using ModelFinder. Branch support was assessed using 1,000 ultrafast bootstrap replicates. The BI analysis was conducted in MrBayes v3.2 (Ronquist et al. 2012), using gene partitions defined by PartitionFinder 2 (Lanfear et al. 2017) (16S: 1–554; COI: 555–1236). Markov Chain Monte Carlo (MCMC) sampling was run for 2,000,000 generations, with trees sampled every 1,000 generations and the first 25% discarded as burn-in. Convergence was considered achieved when the average standard deviation of split frequencies dropped below 0.01.

Acoustic analyses

Advertisement calls of the undescribed species were recorded from the holotype (JXNU 21042833) on 15 June 2021 at a distance of 0.4 m on Mt. Lushan, Jiujiang, Jiangxi Province, China (ambient temperature: 22.3 °C, relative humidity: 85%). Digital recordings were made using a TASCAM DR05X recorder (96 kHz sampling rate, 24-bit depth) with a built-in microphone. The acoustic analysis implemented a Python 3.9 pipeline using *librosa* for audio processing, *noisereduce* for spectral denoising, and *scipy.signal.find_peaks* for pulse detection. Core procedures included amplitude-threshold segmentation at a 0.013 ratio to isolate calls, spectral peak identification for pulse quantification, and dominant frequency extraction via a 512-point Hann-windowed FFT. All parameters were measured following Tapley et al. (2021).

Results

Phylogenetic trees reconstructed using BI and ML methods showed highly consistent topologies. The ML tree is shown in Fig. 1, with node support considered strong when bootstrap values (BS) ≥ 70 or Bayesian posterior probabilities (BPP) ≥ 0.90. Samples of the undescribed species formed a strongly supported monophyletic clade in both analyses (BS = 100; BPP = 1.0). This clade was consistently recovered as sister to *B. mufumontana* (BS = 97; BPP = 1.0). Genetic distances based on the COI and 16S genes, calculated using the uncorrected *p*-distance model, showed that divergence within the undescribed species was below 0.6% for COI and below 0.4% for 16S. The COI gene distance between the undescribed species and its closest related species, *B. mufumontana*, was 8.2%; 10.8% with *B. caudoprocta*; 11.4% with *B. boettgeri*; and 12.1% with *B. liboensis*. For the 16S gene, the closest genetic distance was 1.5% with *B. boettgeri*, 1.7% with *B. mufumontana*, 2.7% with *B. caudoprocta*, and 3.2% with *B. liboensis* (Suppl. material 1: tables S2, S3).

Morphologically, in the PCA analysis, the extracted components PC1 and PC2 explained 62.30% and 25.92% of the variance, respectively, accounting for 88.23% cumulatively. As shown in the scatter plot of PC1 and PC2 (Fig. 2), the undescribed species and *B. mufumontana* are separated without overlapping. Moreover, the undescribed species can be distinguished from all recognized congeners by a unique combination of morphological characters (see Taxonomic account below). Supported by both phylogenetic and morphological evidence, we formally describe it below as a new species.

Taxonomic account

Boulenophrys nebulosa **Shen & Li, sp. nov.**

https://zoobank.org/6BC99CDF-720B-41EA-AE1E-C0216AD3EF6B

Fig. 3, Table 2

Type materials. ***Holotype.*** • JXNU 21042833 (Fig. 3A–F), adult male, collected by Deming Shen, Haiying Zhou, Yifeng Zhong, Chaoyang Wang, Hao Cai, Jun Xu and Shi Xu on 28 April 2021 from Mt. Lushan (29°32.56'N, 115°57.58'E; ca. 970 m a.s.l.), Lushan City, Jiujiang, Jiangxi, China.

Paratypes. (*n* = 6) • JXNU 21042832 (Fig. 4A–C), JXNU 21042834, adult males, and JXNU 21042810, adult female, collected by Deming Shen, Haiying Zhou, Yifeng Zhong, Chaoyang Wang, Hao Cai, Jun Xu and Shi Xu on 28 April 2021 from Mt. Lushan (29°31.87'N, 115°55.87'E; ca. 660 m a.s.l.); • JXNU 21061501(Fig. 4D–F), JXNU 21061502, JXNU 21061504, adult females, collected by same collectors on 15 June 2021 from the type locality (29°32.56'N, 115°57.58'E; ca. 970 m a.s.l.).

Other material examined. • One tadpole (JXNU 21110702; Fig. 5) collected by Haiying Zhou on 2 November 2021.

Etymology. The specific epithet *nebulosa* (feminine of Latin *nebulosus*) refers to the frequently mist-shrouded

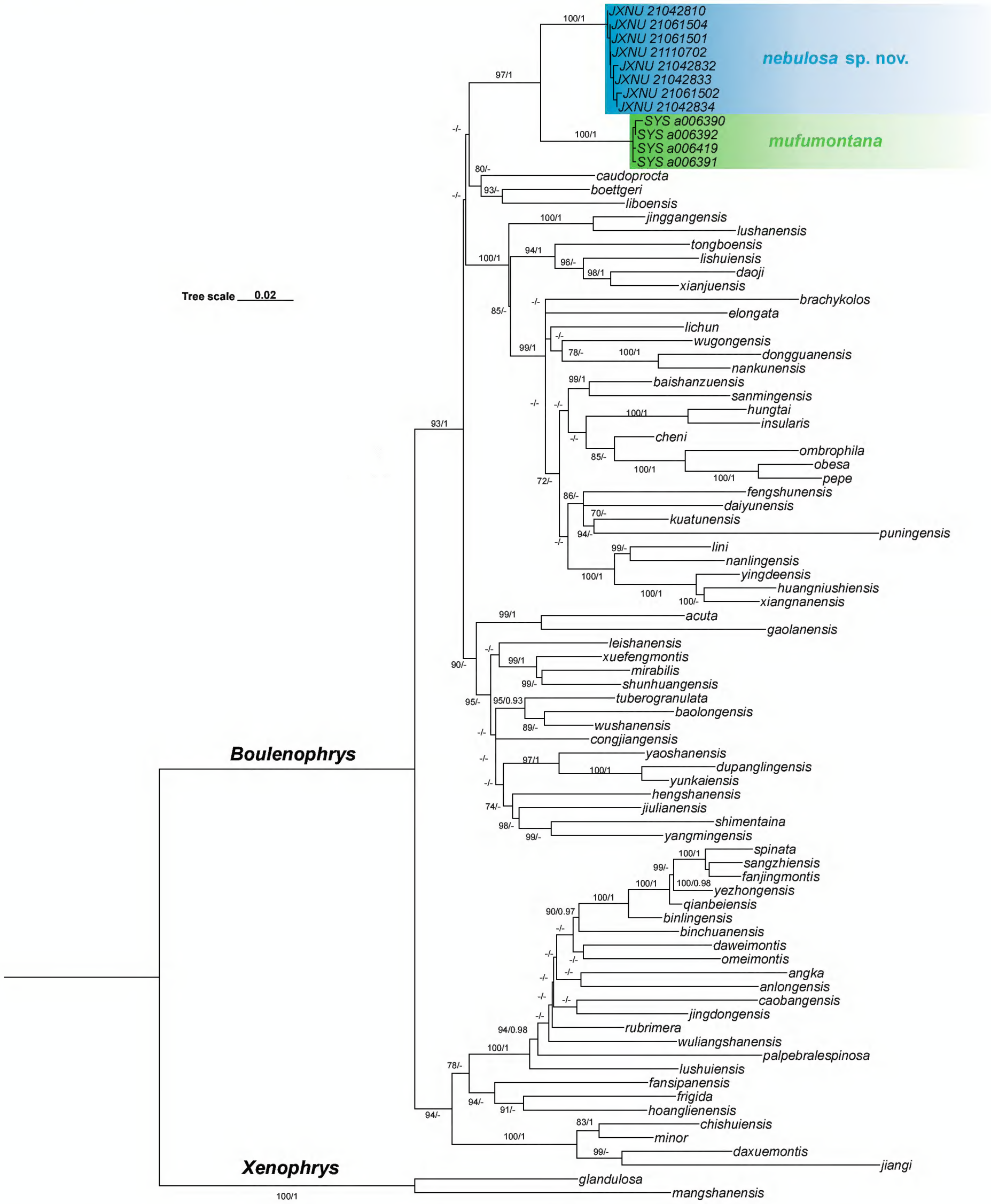

Figure 1. The maximum likelihood topology inferred from partial DNA sequences of the mitochondrial 16S rRNA and COI genes. Bootstrap support values and Bayesian posterior probabilities are shown at the tree nodes. A dash denotes bootstrap support below 70 or Bayesian posterior probability below 0.9.

montane forests above 600 m on Mt. Lushan, Jiangxi Province, China. This name not only reflects the species' habitat preference but also alludes to the region's famous "Cloud & Fog Tea" (云雾茶, yún wù chá) speciality. The English vernacular name "Yunwu Horned Toad" is here proposed, with the corresponding Chinese name "云雾角蟾" (Yúnwù Jiǎochán).

Diagnosis. This species can be distinguished from its congeners by the combination of following morphological characteristics: (1) adult males, SVL 31.8–32.3 mm (n = 3);

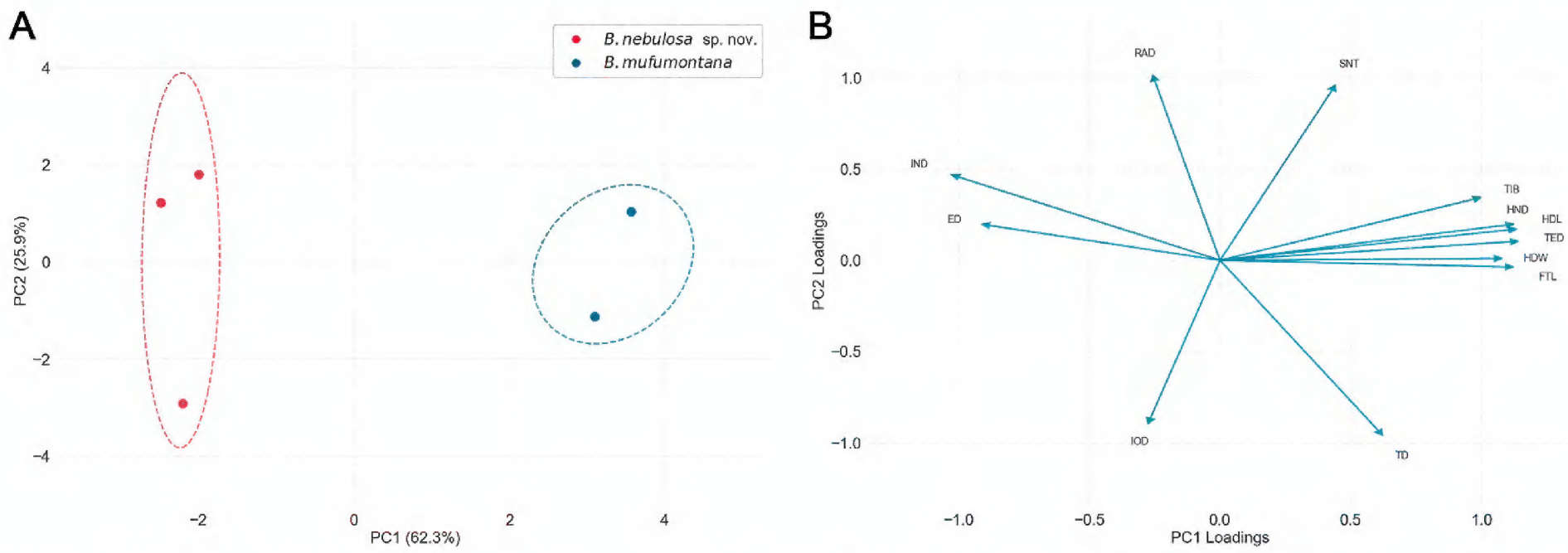

Figure 2. Principal component analysis based on the morphometric measurements of *Boulenophrys nebulosa* sp. nov. and *B. mufumontana*. **A.** Scatter plot of PC1 and PC2; **B.** Loadings plot of PC1 and PC2.

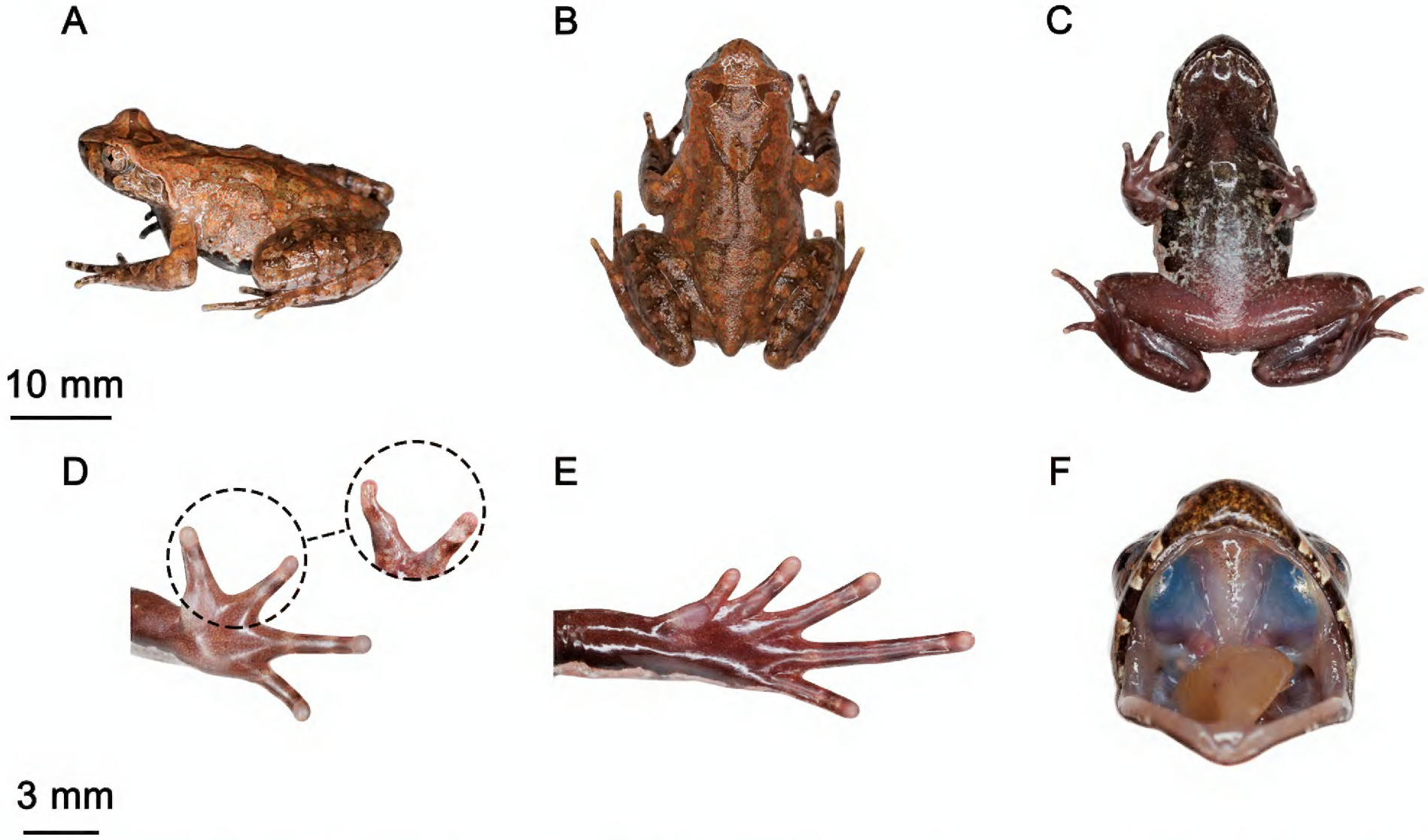

Figure 3. Holotype of *Boulenophrys nebulosa* sp. nov. (JXNU 21042833) in life: **A.** Lateral view; **B.** Dorsal view; **C.** Ventral view; **D.** Volar and dorsal views of left hand; **E.** Plantar view of left foot; **F.** Edge of tongue. Photos by Deming Shen.

Table 2. Measurements (mm) of adult specimens in the type series of *Boulenophrys nebulosa* sp. nov.

	JXNU 21042832	JXNU 21042833	JXNU 21042834	JXNU 21042810	JXNU 21061504	JXNU 21061502	JXNU 21061501
Sex	Male	Male	Male	Female	Female	Female	Female
SVL	31.8	32.2	32.3	37.1	36.5	35	37.3
HDL	10.3	10.6	10.4	12.1	11.5	11.6	11.7
HDW	9.9	9.6	10.3	11.1	11.5	11	11.6
SNT	3.1	3.8	3.4	4.1	4.2	3.9	3.9
IND	3.2	3.3	3.3	3.5	3.6	3.2	3.6
IOD	3.2	2.8	2.8	3	3.6	3.2	3.7
ED	3.8	3.7	4.1	4.1	4.3	4	4.4
TD	1.8	1.5	1.5	2.2	2.1	1.7	1.8
TED	1.1	1.2	1.1	1.4	1	1.4	1.9
HND	6.7	7	7	7.9	7.5	7.5	7.4
RAD	7.3	7.7	7.7	7.9	8.1	8.5	8.6
TIB	14.3	14.5	14.6	16	15.2	16.3	16.7
FTL	13.7	12.7	14.4	14.3	14.4	14.8	14.6

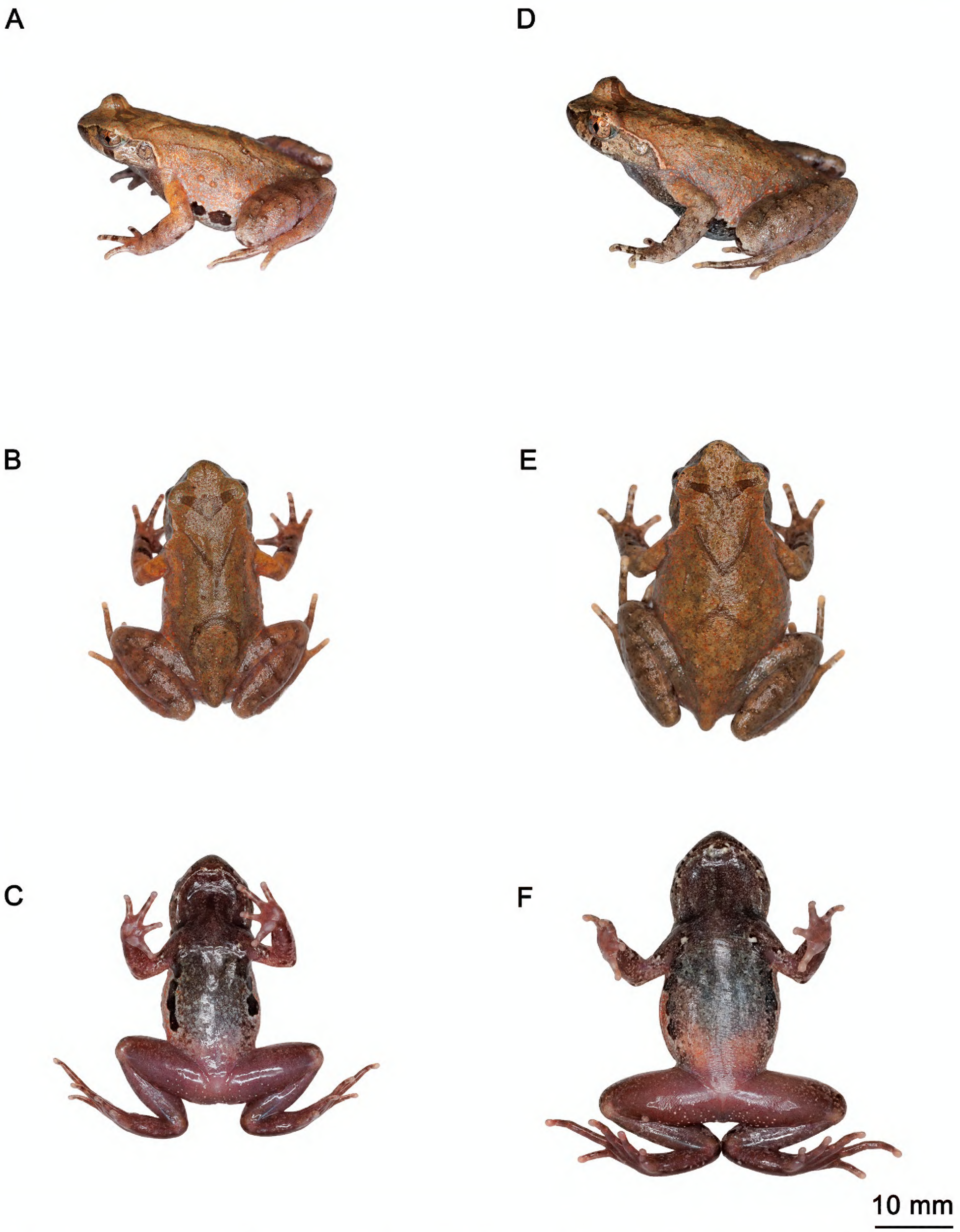

Figure 4. Paratypes of *Boulenophrys nebulosa* sp. nov. in life. Male paratype (JXNU 21042832): **A.** Lateral view; **B.** Dorsal view; **C.** Ventral view. Female paratype (JXNU 21061501): **D.** Lateral view; **E.** Dorsal view; **F.** Ventral view. Photos by Deming Shen.

adult females, SVL 35.0–37.3 mm (n = 4); (2) canthus rostralis well developed, tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak; vomerine teeth present; (5) outer margin of the upper eyelid bears a small, prominent horn-like tubercle; supratympanic fold distinct, narrow, curving posteroventrally to above the arm; (6) relative finger lengths I < II < IV < III; indistinct subarticular tubercle on base of each finger;

(7) heels meeting when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (8) toes with narrow fringes and only rudimentary webbing; (9) rough dorsal skin, a V-shaped, X-shaped or Y-shaped ridge is present on central back of trunk, dorsal surface bears short, irregular and weak ridges, with scattered tubercles and granules, dorsolateral ridges absent; several tubercles on flanks and dorsal hindlimbs; ventral skin smooth with granules; (10) dorsal surface yellowish brown; hollow brown triangular marking between eyes; brown V-shaped, X-shaped, or Y-shaped marking on central back of trunk; dorsal limbs and digits with dark brown transverse bands; and (11) dense nuptial spines on dorsal bases of fingers I and II in breeding adult males, subgular vocal sac present in males.

Description of holotype. JXNU 21042833, adult male, body size small, SVL 32.2 mm; head width slightly smaller than head length, HDW/HDL 0.91; snout rounded in dorsal view, projecting, sloping backward to mouth in profile, protruding well beyond margin of lower jaw; top of head flat; eyes large, ED 0.35 of HDL, pupil vertical, ovoid in natural state; nostril obliquely ovoid; canthus rostralis well developed; loreal region slightly oblique; internasal distance larger than interorbital distance; tympanic region oblique, tympanum moderate in size, margin clear, upper margin in contact with supratympanic fold, TD/ED 0.41; large ovoid choanae at base of maxilla; vomerine ridge weak, vomerine teeth present, maxillary teeth present; margin of tongue rounded, not notched distally; presence of subgular vocal sac.

Figure 5. Tadpole specimen of *Boulenophrys nebulosa* sp. nov. (JXNU 21110702) in preservative: **A.** Lateral view; **B.** Ventral view; **C.** Dorsal view. Photos by Deming Shen.

Forearm length 0.24 of SVL, hand 0.22 of SVL; webbing absent between fingers, lateral fringes absent, relative finger length I < II < IV < III; tips of fingers slightly dilated, round; indistinct subarticular tubercles present; inner metacarpal tubercle observably enlarged, outer one indistinct; single nuptial pad bearing nuptial spines present on dorsal surface of first and second fingers, respectively.

Hindlimbs short, heels meeting when flexed hindlimbs are held at right angles to the body axis; tibiotarsal articulation reaching the center of the eye when the hindlimb is stretched forward along the body; tibiofibular length 0.45 of SVL, foot length 0.39 of SVL; relative toe length I < II < V < III < IV; tips of toes rounded and slightly dilated; toes with narrow lateral fringes and rudimentary webbing; subarticular tubercles indistinct at the base of each toe; inner metatarsal tubercle long and ovoid; outer metatarsal tubercle absent.

Dorsal skin smooth with granules; a discontinuous Y-shaped ridge present on the central dorsum of trunk, discontinuous longitudinal ridges present laterally; several rounded tubercles present on the flanks and dorsal surfaces of the hindlimbs; a prominent, small horn-like tubercle located on the upper eyelid; supratympanic fold distinct, extending from the posterior corner of the eye to above the insertion of the forelimb; tympanum distinct; ventral skin smooth to weakly granular, with spinose tubercles surrounding the cloacal region; pectoral gland small and distinct, located closer to the axilla; a single large femoral gland present on the posterior surface of the thigh, situated approximately midway between the knee and the cloaca.

Coloration of holotype. In life, dorsum yellowish brown, with a hollow brown triangular interorbital marking between eyes and a distinct Y-shaped brown marking at the center of the dorsum, surrounded by indistinct brown netlike pattern; dorsal surfaces of limbs yellowish brown, each bearing several brown transverse bars; axillary region and adjacent lateral flank light yellowish brown; tubercles on the upper eyelids orange; a vertical brown stripe present below the eye, extending from the lower margin of the eye to the upper lip; ventral surface of throat and chest greyish brown, bearing irregular dark brown and white blotches; ventral surfaces of limbs, manus and pes purple, with white blotches; abdominal surface greyish white, scattered with creamy white and orange spots; inner and outer metatarsal tubercles and inner metacarpal tubercle pale purple; pectoral white, digits and femoral glands greyish white; iris light yellowish brown.

In preservative, the dorsum fades from yellowish brown to greyish, while brown markings, including a Y-shaped interscapular marking, a triangular interorbital marking and transverse bands on the dorsal surfaces of the forelimbs and hindlimbs, darken to greyish brown and become more conspicuous. The ventral surfaces fade to greyish white, making the original white spots and blotches more prominent.

Variation. Morphometric data are given in Table 2. All paratypes conform to the holotype in key diagnostic characters but differ in dorsal patterning, ranging from specimens with an indistinct brown netlike pattern as in the holotype to those bearing only an X-shaped interscapular marking and a triangular interorbital marking (e.g., JXNU 21042832). Female paratypes lack nuptial pads and keratinized spines, which are present in males.

Tadpole description. The tadpole was confirmed as *Boulenophrys nebulosa* sp. nov. by molecular phylogenetic analyses. The following tadpole description is based on the specimen JXNU 21110702 at Gosner Stage 29 (Fig. 5). Body depressed and longitudinally oval; TOL 28.0 mm; body width longer than body height, BW/BH 1.3; eyes dorsolateral, pupils round; nostril near eyes; spiracle on the left side of the body and distinct; tail approximately 2.3 times as long as snout-vent length; tail height greater than body height, TAH/BH 1.2; dorsal fin arising just behind tail base, highest near mid-length, tapering gradually to bluntly pointed tip; oral disk terminal; lips expanded, directed upward, forming umbelliform structure; lateral corners of oral disc fold medially, turning upward when not fully extended.

In preservative, the background color of the head and trunk fades from brown to dark brown, interspersed with dark-brown chromatophores, and becomes progressively paler toward the tail tip. Areas lacking white pigmentation contain fewer melanocytes. The belly bears dense white spots, especially concentrated on the chest, while the lateral surfaces of the tail are covered with yellowish-brown spots. BH 2.7; BW 3.6; IOD 2.5; MW 1.6; SL 1.8; SS 3.2; SVL 8.5; TAH 3.3; TAL 19.5; TBW 1.4; TOL 28.0.

Advertisement call. Call descriptions are based on the vocalizations of the male holotype JXNU 21042833. Spectrograms and waveforms are shown in Fig. 6. A total of 13 call groups were analyzed. Each call had an average duration of 120.3 ± 7.4 ms (110.3–135.6 ms) and an average inter-call interval of 487.6 ± 48.8 ms (415.9–573.4 ms). Calls were repeated at a mean rate of 2.05 calls/s (constant repetition rate). Each call consisted of 31.7 ± 2.1 pulses (28–35 pulses). The dominant frequency averaged 3.70 ± 0.08 kHz (3.59–3.84 kHz).

Comparisons. Morphological comparisons between the proposed new species and other recognized species of the genus *Boulenophrys* are provided (Table 3). *Boulenophrys nebulosa* sp. nov. is phylogenetically most closely related to *B. mufumontana*, forming a well-supported sister clade. However, the new species can be readily distinguished from *B. mufumontana* by the following combination of characters: 1) relative finger lengths I < II < IV < III (vs. II = IV < I < III); 2) indistinct subarticular tubercle on base of each finger (vs. distinct subarticular tubercle); 3) larger male body size, SVL 31.8–32.3 mm (vs. 30.1–30.8 mm); 4) heels just meeting when hindlimbs folded (vs. heels overlapping); 5) tibiotarsal articulation reaching the center of eye when leg stretched forward (vs. reaching region between posterior margin of tympanum and center of eye); 6) vomerine teeth present (vs. vomerine teeth absent).

Table 3. Key diagnostic characters for all 78 *Boulenophrys* species.

	Species	SVL in males (in mm)	SVL in females (in mm)	Horn-like tubercle at upper eyelid: larger (T); smaller (F)	Vomerine teeth: present (T); absent (F)	Tongue: notched (T); not notched (F)	Heels overlapping: (T) just meeting (N); not meeting (F)	Lateral fringes on toes: wide (T); narrow (N); absent (F)	Webs on toes: one-fourth (T); rudimentary (N); lacking (F)
1	*B. nebulosa* sp. nov.	31.8–32.3	35.0–37.3	F	T	F	N	N	N
2	*B. acuta*	27.1–33.0	28.1–33.6	T	F	F	F	N	N
3	*B. angka*	31.2–32.1	37.5–39.2	F	F	F	T/N	F	N
4	*B. anlongensis*	40.0–45.5	48.9–51.2	F	F	F	T	N	N
5	*B. baishanzuensis*	28.4–32.4	/	F	F	F	T	N	F
6	*B. baolongensis*	42.0–45.0	/	F	F	T	N	F	F
7	*B. binchuanensis*	32.0–36.0	40.2–42.5	F	F	T/F	N	T	N
8	*B. binlingensis*	45.1–51.0	/	F	F	T	T	/	N
9	*B. boettgeri*	34.5–37.8	39.7–46.8	F	F	T	N	T	N
10	*B. brachykolos*	33.7–39.3	33.9–45.9	F	F	F	F	F	N
11	*B. caobangensis*	34.9–38.9	/	F	F	F	/	F	N
12	*B. caudoprocta*	81.3	/	T	T	F	N	/	N
13	*B. congjiangensis*	28.6–33.4	38.4–40.2	F	F	F	T	N	N
14	*B. changyangensis*	39.4–43.3	/	F	F	F	T	F	F
15	*B. cheni*	26.2–29.5	31.8–34.1	F	F	T	T	T	N
16	*B. chishuiensis*	43.4–44.1	44.8–49.8	F	F	F	T	F	N
17	*B. daiyunensis*	27.6–28.7	33.7–35.6	F	T	F	T/N	N	N
18	*B. daoji*	32.6–33.6	37.5–41.4	F	F	F	F	N	N
19	*B. dalaolingensis*	49.9–56.2	50.3–60.0	F	F	T	T	T	T
20	*B. fanjingmontis*	58.2–63.6	62.8–72.2	F	T	T	N	T	N
21	*B. dongguanensis*	30.2–39.3	/	F	T	F	F	F	N
22	*B. dupanglingensis*	37.8–40.2	41.8–45.9	F	F	F	T	F	N
23	*B. elongata*	28.2–28.5	35.1–37.6	F	T	F	N	N	F
24	*B. hoanglienensis*	37.4–47.6	59.6	F	T	T	/	F	N/F
25	*B. fansipanensis*	30.9–44.3	41.7–42.5	F	T	T/F	/	F	F
26	*B. fengshunensis*	34.3–39.4	42.5–44.9	F	T	F	F	F	N
27	*B. frigida*	30.3–31.8	/	F	T	T/F	/	F	F
28	*B. gaolanensis*	29.2–30.9	32.0–34.9	F	F	F	F	F	F
29	*B. gutu*	34.4–38.0	48.4	F	F	F	F	N	N
30	*B. hengshanensis*	35.7–41.2	37.5–50.2	F	F	F	F	F	F
31	*B. jingdongensis*	53.0–56.5	63.5	F	T	T	T	T	T
32	*B. huangniushiensis*	37.9–40.7	/	F	F	F	T/N	F	F
33	*B. hungtai.*	25.8–33.3	/	F	F	F	F	F	F
34	*B. insularis*	36.8–41.2	47.1	F	T	T	F	F	N
35	*B. jiangi*	34.4–39.2	39.5–40.4	F	F	F	T	F	N
36	*B. jiulianensis*	30.4–33.9	34.1–37.5	F	T	T	T	F	N
37	*B. jinggangensis*	35.1–36.7	38.4–41.6	T	T	F	T	N	N
38	*B. liboensis*	60.5–67.7	60.8–70.6	T	T	T	T	T	N
39	*B. kuatunensis*	26.2–31.4	26.6–37.3	F	F	T	T/F	F/N	F
40	*B. leishanensis*	30.4–38.7	42.3	F	F	F	T	F	N
41	*B. lichun*	33.5–37.0	47.1	F	T	F	F	F	F
42	*B. lushanensis*	40.5–44.7	46.0–50.2	F	T	F	F	N	N
43	*B. lushuiensis*	31.0–34.8	/	F	F	T	/	N	N
44	*B. lini*	34.1–39.7	37.0–39.9	F	F	F	T	T	N
45	*B. lishuiensis*	30.7–34.7	36.9–40.4	F	F	F	/	F	F
46	*B. minor*	34.5–41.2	/	F	F	T	T/N	F	N
47	*B. nanlingensis*	30.5–37.3	/	F	T	T	T	N	N
48	*B. mirabilis*	55.8–61.4	68.5–74.8	T	F	F	T	N	N
49	*B. mufumontana*	30.1–30.8	36.3	F	F	F	T	N	N
50	*B. nankunensis*	29.9–34.9	39.4–41.9	F	T	F	F	F	N
51	*B. omeimontis*	56.0–59.5	68.0–72.5	F	T	T	T	N	N
52	*B. daxuemontis*	41.2–46.2	51.8–58.6	F	F	F	T	N	N
53	*B. obesa*	35.6	37.5–41.2	F	F	F	F	F	N
54	*B. ombrophila*	27.4–34.5	32.8–35.0	F	F	F	F	F	F
55	*B. qianbeiensis*	49.3–58.2	/	F	T	T	T	T	T
56	*B. palpebralespinosa*	36.2–38.0	/	T	T	F	T	T	T
57	*B. pepe*	35.3–36.4	/	F	F	T	F	F	F
58	*B. puningensis*	31.7–34.6	37.8–38.3	F	T	F	F	F	N
59	*B. sangzhiensis*	54.7	/	F	T	T	T	N	N
60	*B. rubrimera*	26.6–30.8	/	F	T	T/F	/	N	F
61	*B. sanmingensis*	27.0–29.5	29.5	F	F	T	T	T	N
62	*B. shuichengensis*	102.0–118.3	99.8–115.6	T	F	T	/	T	T
63	*B. shimentaina*	28.0–30.6	/	F	T	F	T	N	N
64	*B. spinata*	47.2–54.4	54.0–55.0	F	F	T	T	T	T

	Species	SVL in males (in mm)	SVL in females (in mm)	Horn-like tubercle at upper eyelid: larger (T); smaller (F)	Vomerine teeth: present (T); absent (F)	Tongue: notched (T); not notched (F)	Heels overlapping: (T) just meeting (N); not meeting (F)	Lateral fringes on toes: wide (T); narrow (N); absent (F)	Webs on toes: one-fourth (T); rudimentary (N); lacking (F)
65	*B. shunhuangensis*	30.3–33.7	37.6	F	F	F	T	F	F
66	*B. tongboensis*	26.5–31.5	/	F	T	T	T	F	F
67	*B. daweimontis*	34.0–37.0	40.0–46.0	F	T	/	/	F	F
68	*B. tuberogranulatus*	33.2–39.0	50.5	F	F	F	/	F	N
69	*B. wugongensis*	31.0–34.1	38.5–42.8	F	F	F	F	F	N
70	*B. wuliangshanensis*	27.3–31.6	41.3	F	F	T/F	T	F	F
71	*B. wushanensis*	30.4–35.5	38.4	F	F	F	F	F/T	T
72	*B. xiangnanensis*	38.6–42.0	44.4	F	F	F	N	T	N
73	*B. xianjuensis*	31.0–36.3	41.6	F	F	F	T	N	N
74	*B. xuefengmontis*	37.0–38.3	45.3–48.9	F	F	F	T/N	F	F
75	*B. yaoshanensis*	32.5–42.6	46.6–47.4	F	F	F	T/N	F	N
76	*B. yangmingensis*	33.2–37.1	45.2	F	F	F	T	N	N
77	*B. yezhongensis*	41.2–46.2	51.8–58.6	F	T	F	T	N	N
78	*B. yingdeensis*	33.2–35.3	36.3–45.8	F	T	F	T/N	F	N
79	*B. yunkaiensis*	35.3–40.0	45.3–46.1	F	F	F	T/N	F	N

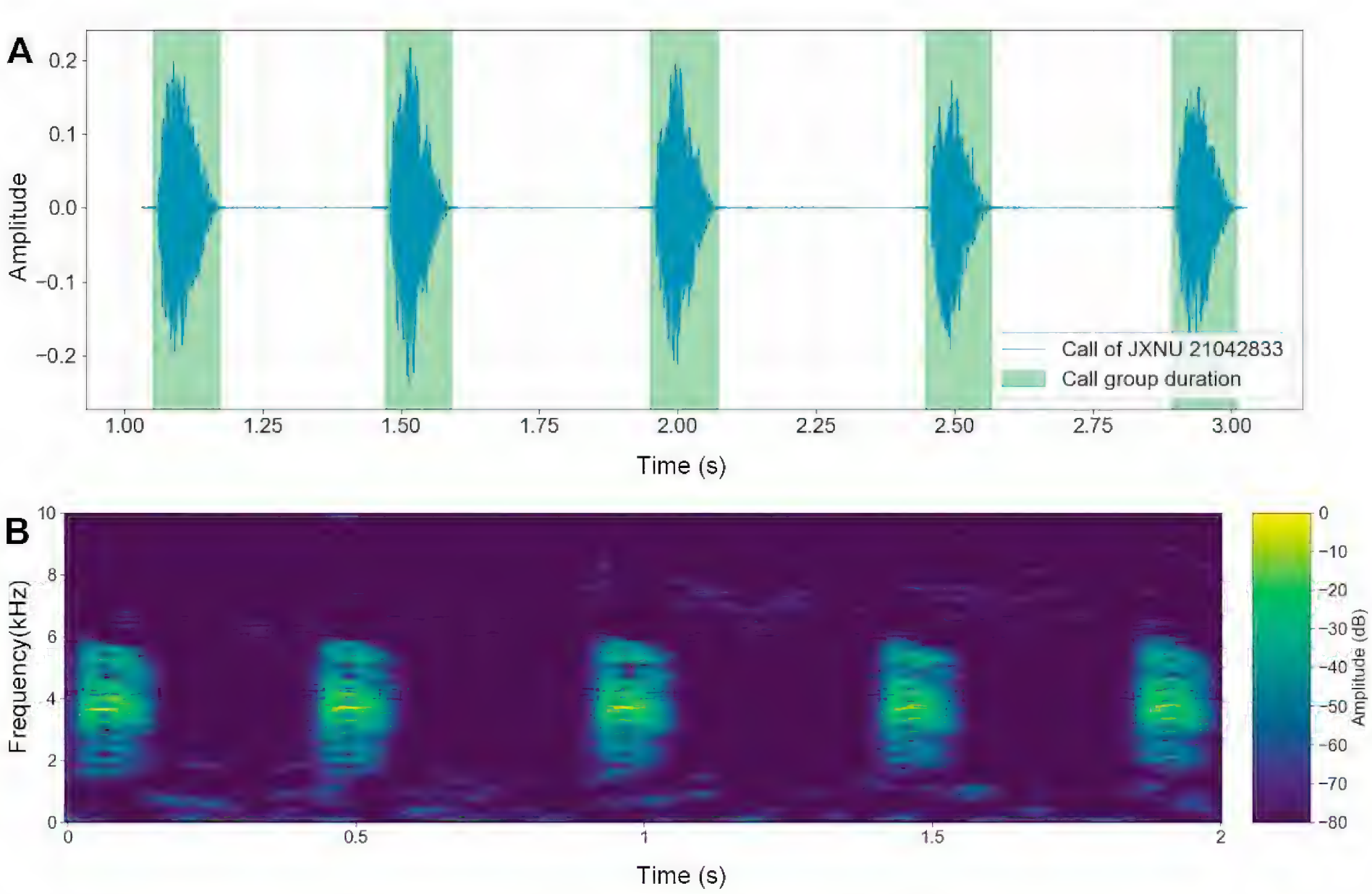

Figure 6. Advertisement call of *Boulenophrys nebulosa* sp. nov. male holotype (JXNU 21042833): **A.** Waveform showing five call groups; **B.** Spectrogram corresponding to the waveform.

The new species differs from *B. boettgeri* by the following combination of characters: 1) smaller male body size, SVL 31.8–32.3 mm (vs. 34.5–37.8 mm); 2) vomerine teeth present (vs. vomerine teeth absent); 3) tongue not notched (vs. tongue notched); 4) fringes on toes narrow (vs. fringes on toes wide); 5) indistinct subarticular tubercle on base of each finger (vs. distinct subarticular tubercle).

Additionally, *Boulenophrys nebulosa* sp. nov. can be distinguished from the following congeners by its heels just meeting when flexed hindlimbs held at right angles to body axis: *B. anlongensis*, *B. baishanzuensis*, *B. binlingensis*, *B. congjiangensis*, *B. changyangensis*, *B. cheni*, *B. chishuiensis*, *B. dalaolingensis*, *B. dupanglingensis*, *B. jiangi*, *B. jingdongensis*, *B. jinggangensis*, *B. jiulianensis*, *B. leishanensis*, *B. liboensis*, *B. lini*, *B. lushanensis*, *B. mirabilis*, *B. nanlingensis*, *B. omeimontis*, *B. palpebralespinosa*, *B. qianbeiensis*, *B. sangzhiensis*, *B. sanmingensis*, *B. shimentaina*, *B. shunhuangensis*, *B. spinata*, *B. tongboensis*, *B. wuliangshanensis*, *B. xianjuensis*, *B. yangmingensis*, and *B. yezhongensis* (vs. heels over-

lapping); and from *B. acuta*, *B. brachykolos*, *B. daoji*, *B. daxuemontis*, *B. dongguanensis*, *B. fengshunensis*, *B. gutu*, *B. gaolanensis*, *B. hengshanensis*, *B. hungtai*, *B. insularis*, *B. lichun*, *B. nankunensis*, *B. obesa*, *B. ombrophila*, *B. pepe*, *B. puningensis*, *B. wugongensis*, and *B. wushanensis* (vs. heels not meeting).

Boulenophrys nebulosa sp. nov. can be distinguished from the following congeners by its fringes on toes narrow: *B. angka*, *B. baolongensis*, *B. caobangensis*, *B. daweimontis*, *B. fansipanensis*, *B. frigida*, *B. hoanglienensis*, *B. lishuiensis*, *B. minor*, *B. tuberogranulatus*, *B. xuefengmontis*, *B. yaoshanensis*, *B. yingdeensis*, *B. yunkaiensis*, and *B. huangniushiensis* (vs. fringes on toes absent); and from *B. binchuanensis*, *B. fanjingmontis*, *B. shuichengensis*, and *B. xiangnanensis* (vs. fringes on toes wide).

For the remaining congeners, *Boulenophrys nebulosa* sp. nov. can be distinguished from *B. elongata* and *B. rubrimera* by its rudimentary webbing on toes (vs. lacking webbing); from *B. caudoprocta* by its horn-like tubercle small at upper eyelid (vs. elongated as triangular appendage); from *B. daiyunensis* by its vomerine teeth present (vs. vomerine teeth absent); and from *B. lushuiensis* by its tongue not notched (vs. tongue notched).

Distribution and habits. *Boulenophrys nebulosa* sp. nov. is currently known only from its type locality, Mt. Lushan, Jiujiang City, Jiangxi Province, China. The species occurs at elevations of 600–1,200 m, primarily in mixed coniferous and broadleaved forests (Fig. 7). Individuals are typically found on the forest floor or under leaf litter near montane streams, as well as along moist roadside drainage channels. Calling males were observed from May to July, all of which were observed calling beneath accumulations of coniferous leaf litter. Females were occasionally observed in drainage ditches lacking flowing water. Tadpoles are observed throughout the year and coexist with the tadpoles of *Quasipaa spinosa* and *B. lushanensis* in some aquatic habitats.

Discussion

The description of *Boulenophrys nebulosa* sp. nov. brings the total number of *Boulenophrys* species recorded in Jiangxi to 15 (Lyu et al. 2023; Shen et al. 2025). Their distributions are shown in Fig. 8, underscoring the high species richness and biogeographic significance of this genus in Jiangxi. Mt. Lushan, located in northern Jiangxi, is an intensely uplifted fault-block mountain formed during the Himalayan orogeny (Gong et al. 2022). Within the massif, heavy rainfall and glacial melt give rise to numerous streams that carve waterfalls, lakes, and deep forest valleys, resulting in a complex mosaic of riparian microhabitats. Moreover, surrounded by the Yangtze River, Poyang Lake water systems, and broad plains, gene flow between Mt. Lushan's amphibians and outside populations is further limited (Li et al. 2015).

Boulenophrys species are reported to exhibit limited dispersal capabilities and depend on specific aquatic habitats. This ecological specialization has not only contributed to the genus's remarkable species diversity but also confined many species to small, localized distributions (Fei et al. 2009; Wang et al. 2019b; Qi et al. 2021). Consequently, the geographic isolation and unique montane stream habitats of Mt. Lushan are expected to drive rapid lineage divergence within *Boulenophrys* populations.

This study provides compelling evidence for recognizing *Boulenophrys nebulosa* sp. nov. as a distinct species, based on an integration of molecular phylogenetics, morphological and morphometric characteristics, tadpole description, call patterns, breeding ecology, and geographic distribution. Acoustic analyses were conducted on the holotype, but they are based on a limited sample size. Frog calls are complex and variable, and broader sampling across individuals and environments would better characterize this variation (Lyu et al. 2024).

At Mt. Lushan, the breeding sites and seasons of *Boulenophrys nebulosa* sp. nov. and *B. lushanensis* overlap, but their reproductive behaviors differ. Males of *B. nebulosa* were recorded calling only under the leaf litter, whereas *B. lushanensis* was more frequently observed on exposed

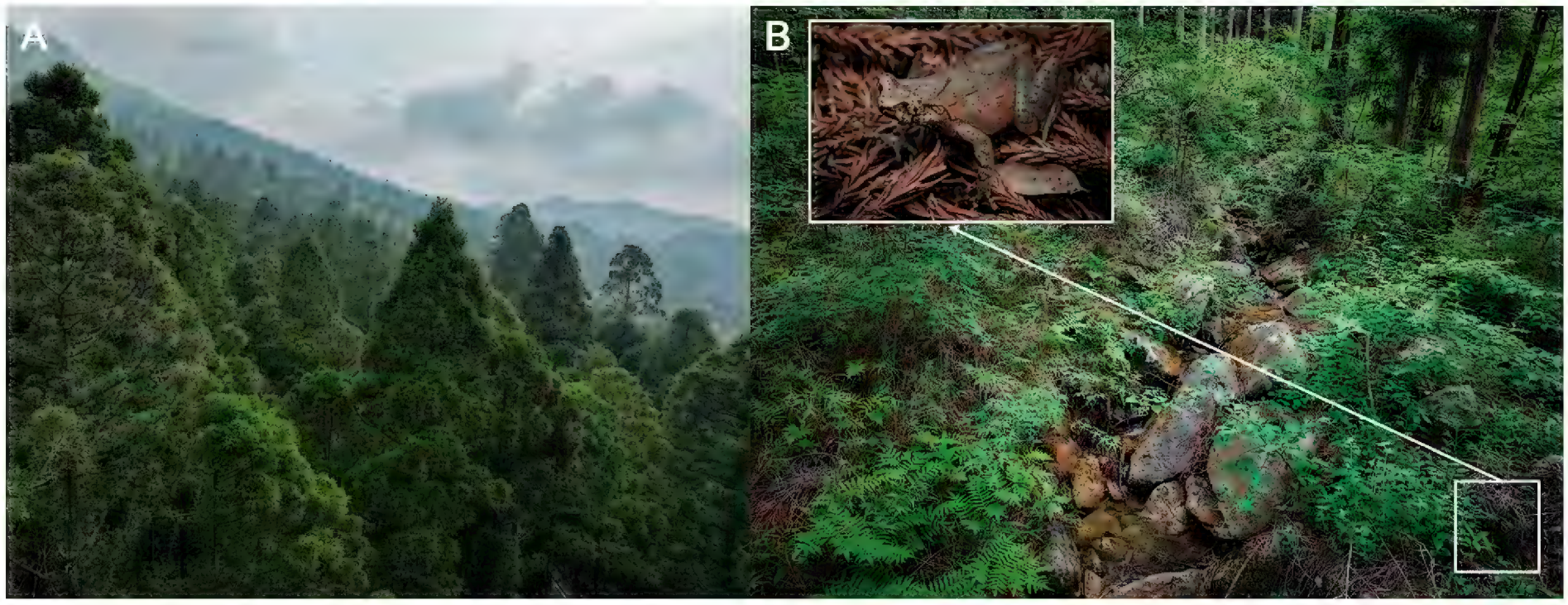

Figure 7. Habitat of *Boulenophrys nebulosa* sp. nov. **A.** Landscape of mixed coniferous and broadleaved forests at the type locality; **B.** Microhabitat showing female paratype (JXNU 21061502) perching on needle litter (white box). Photos by Deming Shen.

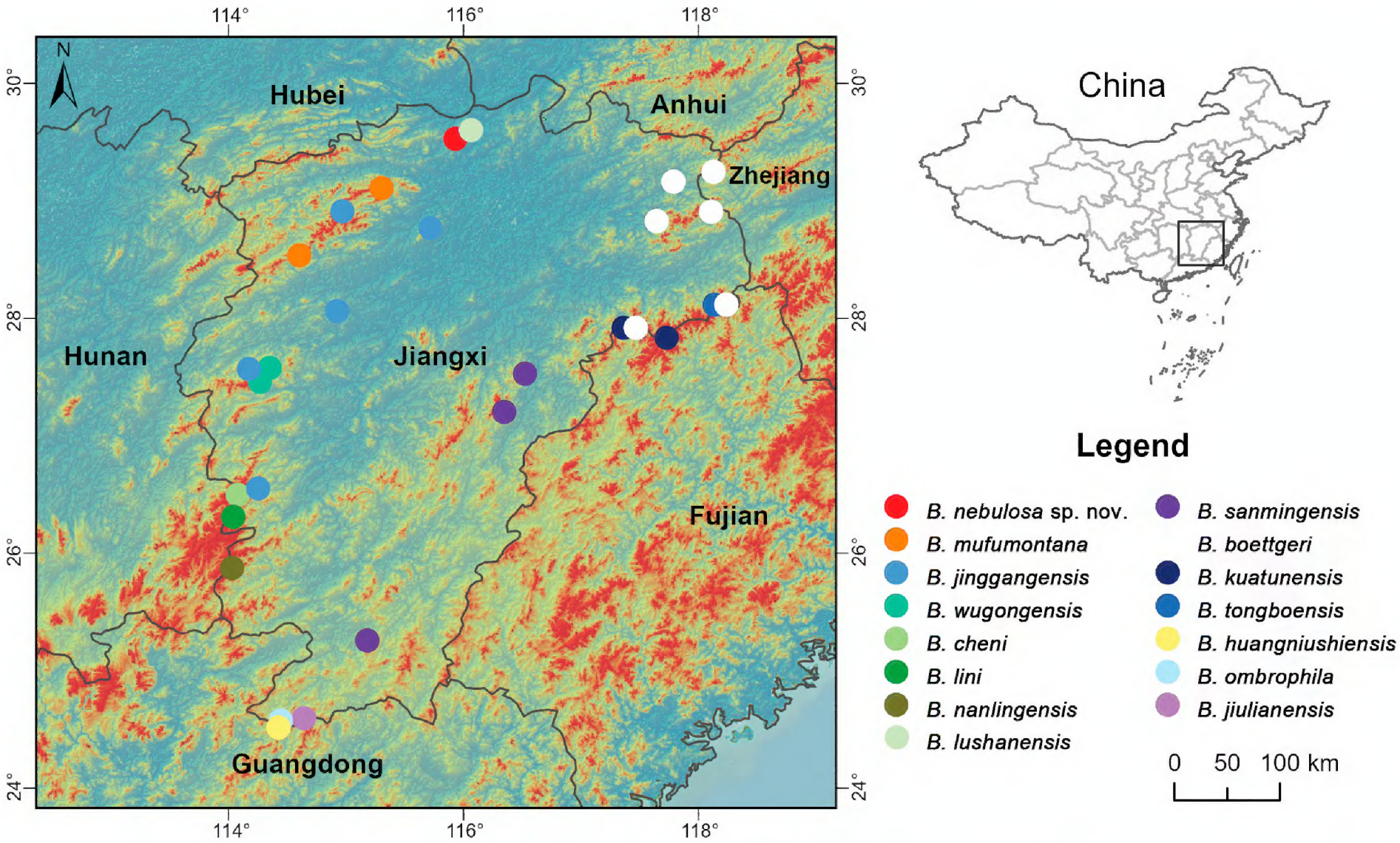

Figure 8. Map showing the distribution pattern of *Boulenophrys* species in Jiangxi Province, China. Distribution sites accessed from Lyu et al. (2023) and Shen et al. (2025).

rocks. These patterns suggest that the two species may occupy distinct ecological niches and that divergence in call characteristics and microhabitat use could contribute to reproductive isolation. Broader acoustic sampling across individuals and environmental contexts will be valuable for testing these hypotheses. Such studies will not only improve our understanding of existing diversity but may also uncover undescribed taxa, providing insights into the evolutionary history of *Boulenophrys* in central China's isolated mountain systems.

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Supplementary material 1

Additional information

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Data type: xlsx

Explanation note: **table S1.** Sample list of genus *Boulenophrys* and outgroups for phylogenetic analysis in this study. **table S2.** Uncorrected *p*-distance (%) among *Boulenophrys* species from the COI. **table S3.** Uncorrected *p*-distance (%) among *Boulenophrys* species from the 16S.

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